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# The Endangered Braun's Bushshrike *Laniarius brauni*: a summary

Michael S. L. Mills<sup>a,b</sup>, Martim Melo<sup>b</sup>, Nik Borrow<sup>c</sup> and Pedro vaz Pinto<sup>d</sup>

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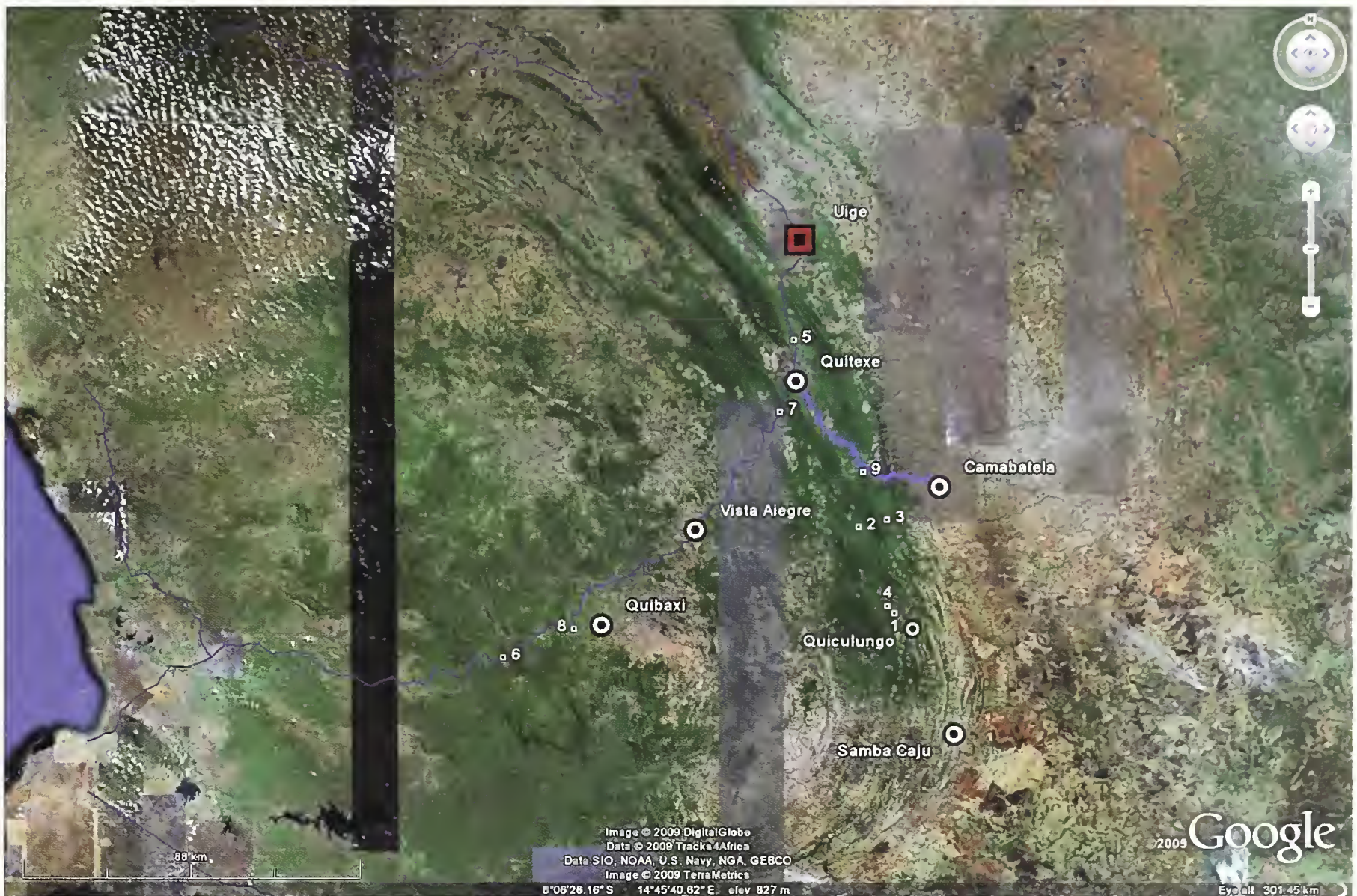
**O picanço de Braun *Laniarius brauni*, espécie 'Em Perigo': uma síntese.** O picanço de Braun *Laniarius brauni* é uma espécie 'Em Perigo' (Lista Vermelha das Espécies Ameaçadas) que apenas ocorre no norte de Angola, numa área inferior a 5.000 km<sup>2</sup>. Aqui revemos a literatura disponível sobre esta espécie, sintetizamos a informação sobre os espécimes conhecidos e apresentamos dados sobre as nossas observações originais. Com estes dados inferimos uma área de ocorrência de 3.500 km<sup>2</sup> e estimamos o tamanho da população em 3.500–7.000 indivíduos adultos (assumindo uma densidade de 1–2 indivíduos/ km<sup>2</sup>). A única estimativa prévia de 498–996 indivíduos adultos baseou-se numa estimativa incorrecta da área de ocorrência. Apesar de ser mais abundante do que se estimava, esta espécie ainda preenche os critérios para a categoria 'Em Perigo' devido à sua distribuição restrita. É provável que a sua área de distribuição seja maior, mas recomendamos que se mantenha a classificação 'Em Perigo' até que sejam obtidos dados que comprovem esta suposição. Esta espécie não existe em nenhuma área protegida, mas parece tolerar alguma perturbação visto mostrar preferência por floresta secundária e bordas de floresta a 600–870 m de altitude. Finalmente, descrevemos em detalhe as vocalizações desta espécie e discutimos a literatura sobre a sua posição sistemática.

**Summary:** The Endangered Braun's Bushshrike *Laniarius brauni* is restricted to an area of less than 5,000 km<sup>2</sup> in northern Angola. We review previous literature on this species, summarise information on specimens and provide details of our own unpublished records. From this we calculate a range size of 3,500 km<sup>2</sup> and, based on the assumption of a mean density of 1–2 individuals/km<sup>2</sup>, calculate a population size of 3,500–7,000 mature individuals. The only previous population size of 498–996 individuals was based on an erroneous range size. Despite being more numerous than previously estimated, and potentially more widespread, it still meets criteria for Endangered status based on range size. We recommend that it retains Endangered status pending the collection of further field data. The species does not occur in any conservation area, although it is perhaps tolerant of some habitat disturbance, favouring secondary forest and forest edge at 600–870 m. Finally, we describe in greater detail its vocalisations and discuss its systematic treatment in the literature.

**T**he Endangered Braun's Bushshrike *Laniarius brauni* has a range of <5,000 km<sup>2</sup>, limited to Cuanza Norte and Uíge provinces in northern Angola (Fry & Keith 2000, BirdLife International 2008, Fry 2009). Owing to its restricted distribution, even tiny errors in reported localities can distort accurate estimation of range size. Several inaccuracies and unsubstantiated claims exist in the literature, and are outlined below. Here we summarise fully details of specimens and review previous literature on the species, providing locality data as accurately as possible. We also present new and precise information from our own field observations. Finally, we provide a fuller description of the species' vocalisations, which were described only briefly by Heinrich (1958) and Sinclair *et al.* (2007), and discuss its systematic treatment.

## Collection localities and recent sightings

Braun's Bushshrike was first collected on 17 April 1936 near Quiculungo (08°31'S 15°19'E; c.800 m; also Quiculungo or Quicolungo; see Fig. 1) by Rudolf H. Braun. The specimen was sent to the Berlin Museum, where Erwin Stresemann tentatively described it as the male of Gabela Bushshrike *L. [luehderi] amboimensis*, then known only from a female specimen (Stresemann 1937). In 1939 Braun collected four additional specimens at Quiculungo, including females, and Stresemann soon realised his error. He invited David Bannerman to describe the new taxon, based on these four new specimens, two males and two females (Bannerman 1939). These four specimens, but not that collected in 1936, were sent to the British Museum and are still housed there (see Table 1). Bannerman (1939) described the new subspecies *Laniarius*



**Figure 1.** A Google Earth (2009) image of record localities (small squares) and important towns (circles) within the range of Braun's Bushshrike *Laniarius brauni*. Most records are from a distinctive area of forest habitats running *c.* 150 km north–south, from *c.* 40 km north-west of Uíge to *c.* 20 km south of Quiculungo. From Vista Alegre westwards is another block of forest, although much of this lies below 600 m, the lower altitudinal limit of Braun's Bushshrike. Localities: 1 = type locality, 6 km north-west of Quiculungo; 2 = Roça Canzele; 3 = 15 km south-west of Camabatela; 4 = Bolongongo; 5 = 30 km south of Uíge; 6 = Dembos forest; 7 = 20 km south of Quitexe; 8 = 7 km west of Quibaxi; 9 = rio Dange. Blue and purple lines indicate roads.

**Figura 1.** Uma imagem do Google Earth (2009) com as localidades de registo (quadrados) e povoações importantes (círculos) na área de distribuição do picão de Braun *Laniarius brauni*. A maior parte dos registos provêm de um tipo de floresta distinto que se estende na direcção norte-sul ao longo de cerca de 150 km, a partir de cerca de 40 km a noroeste de Uíge até cerca de 20 km a sul de Quiculungo. De Vista Alegre para oeste existe outro bloco de floresta, mas a maior parte encontra-se abaixo dos 600 m, a altitude mínima a que ocorre o picão de Braun. Localidades: 1 = localidade tipo, 6 km a noroeste de Quiculungo; 2 = Roça Canzele; 3 = 15 km a sudoeste de Camabatela; 4 = Bolongongo; 5 = 30 km a sul de Uíge; 6 = floresta de Dembos; 7 = 20 km a sul de Quitexe; 8 = 7 km a oeste de Quibaxi; 9 = rio Dange. Linhas azuis e roxas indicam estradas.

*luehderi brauni*, for its collector Braun. It should be noted that the locality details in the type description, 'Quicolungo, Angola, circa 09°50'S 15°20'E, south of the Cuanza River' (Bannerman 1939) match those given by Sick (1934) and are erroneous; Stresemann (1937) corrected Sick's (1934) error to 08°29'S 15°16'E, but Bannerman (1939) overlooked this (Traylor 1962). This locality is *c.* 6 km north-west of Quiculungo town, and just 2–3 km south-east of Bolongongo (08°28'S 15°15'E).

Braun collected another specimen in 1945 and two more in 1946. Then, in 1954–57, Gerd

Heinrich collected a series of 13 specimens, bringing the total to 21 (Table 1). The last record of the species in the 20th century was in November 1957. Extraordinarily, based on the specimens we have traced and a thorough review of the literature (Dean 2000; W. R. J. Dean unpubl. data), prior to 2005 the species was known from the records of just two people, Braun and Heinrich. In addition to the type locality, specimens were taken at (based on information in museum catalogues):

- rio Dange: 08°09'S 15°12'E, 810 m, *c.* 20 km west of Camabatela (08°12'S 15°22'E);

**Table 1.** A chronological list of the 21 specimens of Braun's Bushshrike *Laniarius brauni* we have traced. All are of adult specimens. Locality data is given according to the relevant museum catalogues in inverted commas, followed by the locality name we use. Museum abbreviations as follows: AMNH = American Museum of Natural History, New York; BMNH = British Museum of Natural History (now The Natural History Museum), Tring; FMNH = Field Museum of Natural History, Chicago; NMNH = Smithsonian Institution, Washington DC; YPM = Yale Peabody Museum of Natural History, New Haven; ZMB = Museum für Naturkunde, Berlin; ZMH = Zoologisches Museum Hamburg.

**Tabela 1.** Uma lista cronológica dos 21 espécimes de picanço de Braun *Laniarius brauni* que conseguimos localizar. Todos os espécimes são de adultos. O nome da localidade dada por cada museu está entre aspas e é seguido do nome da localidade dado por nós. As abreviações dos nomes de museus são: AMNH = American Museum of Natural History, New York; BMNH = British Museum of Natural History (actualmente: The Natural History Museum), Tring; FMNH = Field Museum of Natural History, Chicago; NMNH = Smithsonian Institution, Washington DC; YPM = Yale Peabody Museum of Natural History, New Haven; ZMB = Museum für Naturkunde, Berlin; ZMH = Zoologisches Museum Hamburg.

Date collected / Data da colheita	Collector / Colector	Museum / Museu	Specimen no./ Espécime nº	Location / Localidade	Sex
17 April 1936	Braun	ZMB	36.1061	'Quicolungo'; 6 km north-west of Quiculungo	M
*11 April 1939	Braun	BMNH	1939.8.4.1	'Quicolungo, Angola; -8.45/15.28'; 6 km north-west of Quiculungo	M
22 March 1939	Braun	BMNH	1940.12.2.13	'Quicolungo, Angola; -8.45/15.28'; 6 km north-west of Quiculungo	F
1 April 1939	Braun	BMNH	1940.12.2.14	'Quicolungo, Angola; -8.45/15.28'; 6 km north-west of Quiculungo	F
23 April 1939	Braun	BMNH	1940.12.2.12	'Quicolungo, Angola; -8.45/15.28'; 6 km north-west of Quiculungo	M
4 May 1945	Braun	ZMB	49.25	'Roça Alto Dange'; assumed to be Dange River	F
27 November 1946	Braun	AMNH	344028	'Camabatela, Dange River'; Dange River	M
29 November 1946	Braun	AMNH	344027	'Camabatela, Dange River'; Dange River	M
6 April 1954	Heinrich	FMNH	221265	'Canzele, 30 km W Camabatela'; Roça Canzele	M
**6 May 1954	Heinrich	FMNH	221264	'Canzele, 30 km W Camabatela'; Roça Canzele	M
**6 May 1954	Heinrich	AMNH	800773	'Cantele, Qual Sul R.'; Roça Canzele	M
27 March 1955	Heinrich	ZMH	58.500	'N-Angola, 15 km S v. Camabatela'; 15 km south-west of Camabatela	F
27 March 1955	Heinrich	ZMH	58.501	'N-Angola, 15 km S v. Camabatela'; 15 km south-west of Camabatela	F
30 March 1955	Heinrich	FMNH	225389	'Camabatela, 15 km SW'; 15 km south-west of Camabatela	M
1 April 1955	Heinrich	FMNH	225390	'Camabatela, 15 km SW'; 15 km south-west of Camabatela	F
1 April 1955	Heinrich	ZMH	58.499	'N-Angola, 15km S v. Camabatela'; 15 km south-west of Camabatela	M
17 September 1957	Heinrich	NMNH	583410	'Roca Canzele, North of Quiculungo, 600 m'; Roça Canzele	M
21 October 1957	Heinrich	NMNH	583411	'Roca Canzele, North of Quiculungo, 700 m'; Roça Canzele	M
21 October 1957	Heinrich	NMNH	583412	'Roca Canzele, North of Quiculungo, 700 m'; Roça Canzele	F
28 October 1957	Heinrich	YPM	YPM 95206	'Cuanza Norte Province. Elev. 1969 feet, -8.467 15.267'; Bolongongo	F
30 October 1957	Heinrich	YPM	YPM 95205	'Cuanza Norte Province. Elev. 1969 feet, -8.467 15.267'; Bolongongo	M
16 November 1957	Heinrich	NMNH	583413	'Bolongongo, North of Quiculungo, 700 m'; Bolongongo	M

\*the type specimen

\*\* refers to the same specimen, first sent to the FMNH and later exchanged with AMNH

- Roça Canzele: 08°17'S 15°11'E, 870 m (Dean 2000), c.25 km north of Quiculungo, 27 km west of Camabatela and 9 km south-west of the rio Dange; sometimes spelt Cantele or Canzela;
- 15 km south-west of Camabatela: c.08°16'S 15°15'E, 830 m, and c.7.5 km east of Roça Canzele; and
- Bolongongo: 08°28'S 15°15'E, 870 m, just 2-3 km west of the type locality.

We have assumed, based on its name, that Roça Alto Dange (see Table 1) must be on the Dange River and hence treat the locality as the rio Dange, from where there are two other

specimens. These are the only specimen localities, despite Camabatela being listed as a known locality by Dean (2000) and Fry (2009). This is particularly important because Camabatela is located in grassland and open woodland, with no suitable habitat for Braun's Bushshrike within 10 km of the town.

In addition, Chapin (1954) reported the species from Quibaxi (08°30'S 14°35'E) to Camabatela, citing Rudolf Braun (pers. comm.) but provided no supporting evidence. Pinto (1960) also mentions that it occurs in the Dembos area (a municipality based on Quibaxi; also Quibaxe), but no source is given. It should be noted, however, that we have now recorded the species from Quibaxi

(details below). Finally, Dean (2001) mentions a possible record of Braun's Bushshrike from near Dondo (09°41'S 14°25'E), based on the presumed misidentification of an out-of-range report of Crimson-breasted Shrike *L. atrococcineus* from nearby Bom Jesus (09°10'S 13°34'E, 50 m) in Günther & Feiler (1986). Because the observers did not mention the possibility of the record belonging to Braun's Bushshrike, and the record comes from 160 km south of Braun's Bushshrike's known range and well below its known elevational range (which is 600–870 m), this record can safely be assumed not to refer to Braun's Bushshrike. Consequently, the suggestion that it occurs in Kissama National Park (Dean 2001, BirdLife International 2008) no longer holds; the species does not occur in any conservation unit.

Then, in January 2005, Braun's Bushshrike was found for the first time in 48 years along the main road south of Uíge town, Uíge province, in degraded forest (Sinclair *et al.* 2007). This locality has been reported as both '30 km south of Uíge' (I. Sinclair *et al.* in *Bull. ABC* 12: 177) and 'the approach to Uíge town', '40–60 km north-east of the type locality' (Sinclair *et al.* 2007). The correct locality is *c.*30 km south of Uíge town and 5–10 km north of Quitexe (07°56'S 15°02'E; PVP pers. obs.) at *c.*07°51'S 15°02'E (680 m); this is *c.*80 km *north-west* of the type locality. The next available sightings, in November 2005, were by NB & PVP from Dembos forest at 08°35'S 14°21'E, 650 m, *c.*100 km south-west of Quitexe, Cuanza Norte province, extending the known range significantly, if the reports by Chapin (1954) and Pinto (1960) are discounted. Finally, in August 2009 MSLM & MM spent three days in forests in the Bolongongo and Quiculungo areas, and driving from Camabatela west to Quitexe, passing within 10 km of Roça Canzele. No Braun's Bushshrikes were found in this region, despite use of playback of the very similar Luehder's Bushshrike *Laniarius luehderi* vocalisations (see Vocalisations). However, four pairs were quickly found 20 km south of Quitexe at 08°01'S 15°00'E (790 m), also in degraded forest, and a single bird was heard *c.*7 km west of Quibaxi at 08°31'S 14°31'E (780 m). To our knowledge, these are the only records other than the specimens discussed above. The species' altitudinal range has been stated as 600–1,265 m (Fry 2009). We are unable to trace the source of

this information, and all records mentioned herein are from 600–870 m, which should be regarded as the species' altitudinal range until further data become available.

### Habitat, range, population size and threat status

Although Braun's Bushshrike is typically regarded as a forest species, Heinrich (1958) described its favoured habitat as densely overgrown, liana-rich gallery forest, and thickets at the edges of clearings in more extensive forest. He concluded that it shunned the interior of primary forest. Our records agree with this and the reports in Traylor (1962; no source is given), with all of our sightings being from secondary forest or forest edge, although we surveyed few areas of primary forest. These observations suggest that the species is at least tolerant of, and may even favour, disturbed forest. However, complete clearance of forest understorey for agriculture is widespread within its range and appears to render the habitat unsuitable for Braun's Bushshrike, so habitat modification remains a significant threat.

The only previous range size estimate is of an Extent of Occurrence of 4,600 km<sup>2</sup> (BirdLife International 2000, 2008). Using the updated information presented herein, we suggest by the same definition a range of *c.*3,500 km<sup>2</sup>, smaller than that estimated by BirdLife International (2008) because we reject the possible record from



**Figure 2.** The bright orange breast of Braun's Bushshrike *Laniarius brauni* distinguishes it from the chestnut-breasted Luehder's Bushshrike *L. luehderi* (Nik Borrow)

**Figura 2.** O cor-de-laranja vivo do peito do picanço de Braun *Laniarius brauni* permite distingui-lo do picanço de Luehder *L. luehderi* cujo peito é castanho (Nik Borrow)

near Dondo (Dean 2001), 160 km to the south. However, further records will almost certainly reveal the species to be more widespread. Satellite imagery from Google Earth (2009, <http://earth.google.com/>) reveals a distinctive area of forest habitat running c.150 km north–south, from 07°16'S to 08°34'S, and 40 km east–west, between 15°20'E and 14°42'E, much of it within the known altitudinal range of Braun's Bushshrike (600–870 m). There is also a large block of more open forest south-west of this, although much of the latter lies below 600 m (Fig. 1). These forests need to be explored more extensively to establish the species' true range and habitat requirements.

Owing to the paucity of records, it is impossible to estimate the species' general abundance. However, Heinrich (1958) found that each 'finger' of forest penetrating the grasslands west of Camabatela had one or several pairs of Braun's Bushshrikes, and 3–4 pairs were found by both Sinclair *et al.* (2007) and MSLM & MM within a small area. These records suggest that the species is generally common in suitable habitat, although PVP considers that it is much less common than Gabela Bushshrike is on the central scarp. Importantly, however, it should be noted that the population estimate by BirdLife International (2008) of 498–996 individuals is based on the wrong range size—460 km<sup>2</sup> instead of 4,600 km<sup>2</sup>—and hence is an order of magnitude smaller than it should be. Using the same assumption of 1–2 individuals / km<sup>2</sup> and our own range estimate, we calculate a population size of 3,500–7,000 individuals.

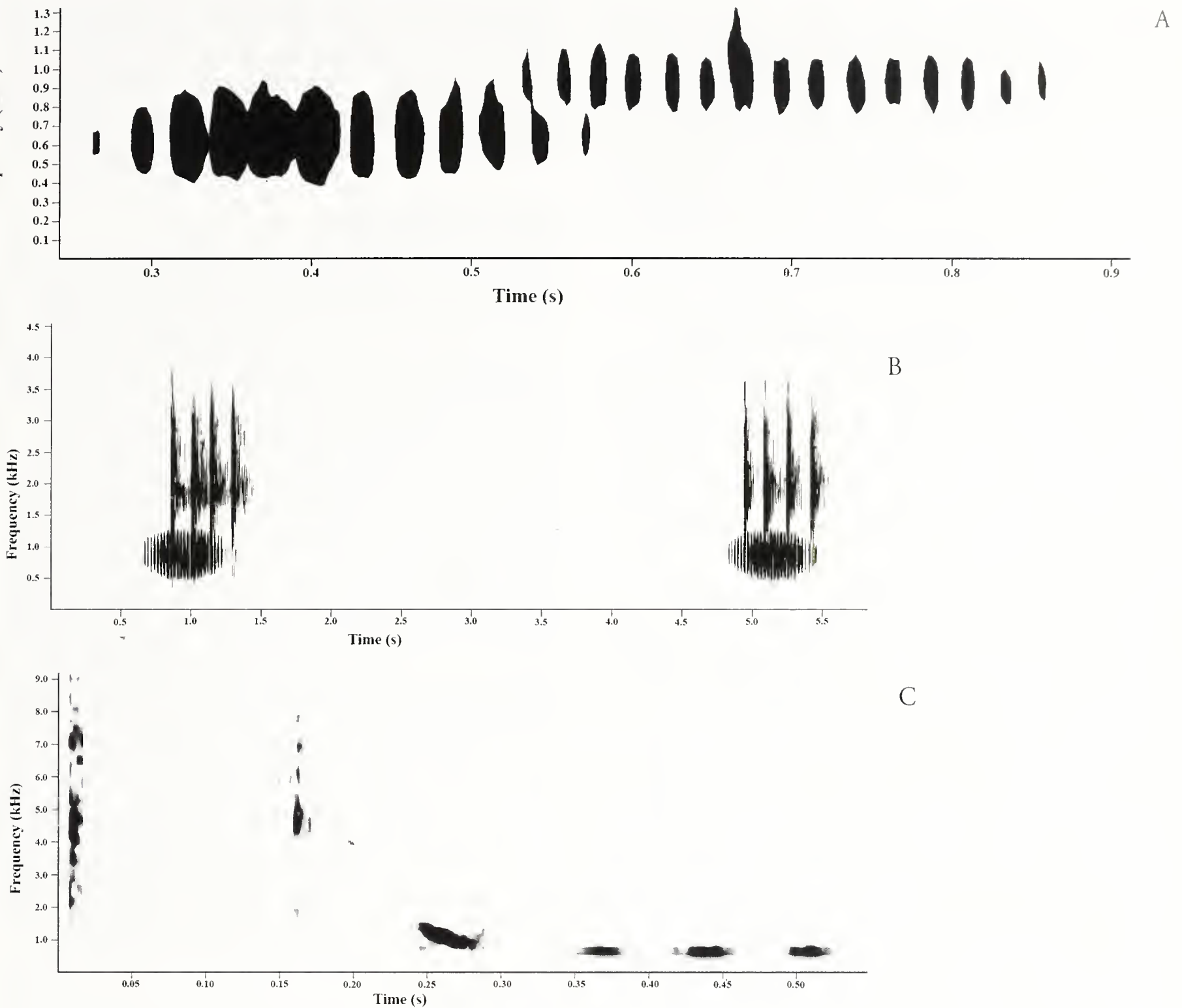
The species is currently listed as Endangered, meeting criteria B1, of having an Extent of Occurrence of <5,000 km<sup>2</sup>, and C, of having a population size estimated at <2,500 mature individuals (BirdLife International 2008). Based on our population estimate of 3,500–7,000 individuals, it no longer meets Endangered species status for small population size. However, the known range is still smaller than 5,000 km<sup>2</sup>, within which its population may be fragmented and declining. Although we expect Braun's Bushshrike to be more widespread and numerous than is currently known, and the species may warrant downlisting to Vulnerable, we recommend this be done only when proof is available, in the form of field data from new localities that extend the known range.

## Vocalisations

Owing to the species' skulking nature (Heinrich 1958), knowledge of its vocalisations is important for future surveys of Braun's Bushshrike. Playback of calls by NB & MSLM elicited excited responses from birds, so playback of vocalisations should be used in future surveys. Heinrich (1958) described the calls as distinctive and consisting of (i) a short, low, far-carrying growl (*kurr* or *urr*) given individually, between long pauses, (ii) two soft notes followed by two loud notes, rendered *didi – dudu*, (iii) a loud sharp, *tschäkdudodeder* when disturbed, and (iv) a repeated, loud, sharp *tschäk... tschäk... tschäk* in warning. Sinclair *et al.* (2007) describe the bird's voice as deep and guttural and 'very similar to both Luehder's *L. luehderi* and Gabela Bushshrike *L. amboimensis*, both in their contact-calls and duetting song'. Chapin (1954), although he never saw the species himself, wrote 'it has a voice much less pleasing than that of [Southern Boubou, probably referring to the Tropical / Swamp / Southern Boubou complex] *L. ferrugineus*, and similar no doubt to that of nominate *luehderi*'. Finally, Harris & Franklin (2000) give some further descriptions, repeated in Fry (2009), but we are unaware of the source of these.

NB & MSLM made sound-recordings of Braun's Bushshrike during our field observations; those of MSLM are archived at the British Library Sound Archive and will be published on Mills (in prep.). These recordings were copied digitally, edited with Goldwave software ([www.goldwave.com](http://www.goldwave.com)), inspected aurally, and used to produce sonograms with Raven Lite software (Cornell Lab of Ornithology 2003–05). Recordings and sonograms were compared to vocalisations of Gabela Bushshrike presented on Mills (2007) and described by Ryan *et al.* (2004) and Mills (2009), and of Luehder's Bushshrike presented on Chappuis (2000) and discussed by Mills (2009).

The commonest vocalisation is a low-pitched growl or croak, emitted at regular intervals. This call is analogous to the '*worrrk*' call of Gabela Bushshrike (Ryan *et al.* 2004). The rate of delivery (seconds between calls) varied significantly; of three recordings made of 50 seconds or longer, the slowest delivery was every 4.7 seconds. However, when excited by playback, birds increased the rate of delivery to an average of every 1.7 seconds ( $n = 1$  recording of 97 seconds). Limited observations



**Figure 3.** Sonograms of the vocalisations of Braun's Bushshrike *Laniarius brauni*. A: two croak / growl calls delivered at different frequencies, by different birds calling simultaneously. B: duet, with the presumed male giving a croak / growl call and the female a series of loud clicks. C: threat / display-flight calls of the male: two harsh clicks, followed by four melodious whistles, the first whistle higher pitched than the following three.

**Figura 3.** Sonogramas das vocalizações do picanço de Braun *Laniarius brauni*. A: dois tipos de 'grasnar' emitidos em diferentes frequências por vários indivíduos ao mesmo tempo. B: dueto, com o macho presumido a grasnar e a fêmea a emitir uma série de estalidos altos. C: vocalizações de ameaça e/ou de voo de parada do macho: dois estalidos ásperos, seguidos por quatro assobios melodiosos, dos quais o primeiro com a frequência mais elevada.

reveal both the pitch and duration of this call to be variable, with pitch varying between at least 0.65 kHz (mean; range 0.4–0.9 kHz) and 0.95 kHz (0.8–1.1 kHz; Fig. 3a). These frequencies overlap with those of the analogous calls of Luehder's and Gabela Bushshrikes (Dowsett-Lemaire 1990, Mills 2009), and these calls cannot be used to differentiate the species. The croak / growl is also given in duet by one member of a pair (thought to be the male because of its more aggressive responses), while the other bird makes a series of 4–10 loud clicks, like the *tschäk... tschäk... tschäk*

warning call described by Heinrich (1958) and similar to that of Luehder's Bushshrike (Chappuis 2000) (Fig. 3b). The only other vocalisation heard by us during field observations was a series of notes given during a short, slow threat / display-flight, in which the presumed male alternated between exaggerated flapping and gliding, with its back feathers puffed-out. This display-flight is similar to that made by Swamp Boubou *Laniarius bicolor* (Fry & Keith 2000). The sequence commences with one or two harsh clicks, followed by four melodious whistles, the first whistle higher pitched

than the following three (Fig. 3c). No other melodious whistles, like those commonly made by Gabela and Luehder's Bushshrikes, were heard. However, our observations may not account for the full vocal repertoire of Braun's Bushshrike, and the second call described by Heinrich (1958) may be of a melodious whistle similar to those of Gabela and Luehder's Bushshrikes.

### Systematic treatment and nomenclature

The *Laniarius luehderi* complex comprises four generally recognised taxa: the similar *luehderi* and *castaneiceps* races which are always treated as subspecies of Luehder's Bushshrike *L. luehderi*, and the distinctive *brauni* and *amboimensis* whose systematic treatment has varied. Bannerman (1939) described *brauni* as a subspecies of *L. luehderi*, but remarked that it was 'extremely tempting to give it the status of a full species' due to its distinctive plumage. This treatment of *brauni* as a subspecies of *luehderi* has been followed in much of the literature (Hall & Moreau 1960, White 1962, Collar & Stuart 1985, Howard & Moore 1991, Dowsett & Dowsett-Lemaire 1993, Harris & Franklin 2000, Dickinson 2003). Hall & Moreau (1960) considered *brauni* and *amboimensis* as incipient species whose status requires verification. Sibley & Monroe (1990) were the first to give *brauni* and *amboimensis* species status; they regarded them as allospecies, i.e. members of the *L. luehderi* superspecies. This treatment has been followed in most recent works (Clements 1991, Monroe & Sibley 1993, Collar *et al.* 1994, Fry & Keith 2000, BirdLife International 2008, Fry 2009, Gill *et al.* 2009). Given the distinct plumages of *brauni* and *amboimensis*, we recommend their treatment as full species until such time as a robust and complete phylogeny becomes available. Nguembock *et al.* (2008) constructed molecular phylogenies for most of the genus *Laniarius*, showing that plumage coloration is generally not a reliable character for defining species limits in the genus. Blood samples are now available for Gabela Bushshrike, but not yet for Braun's Bushshrike.

There is also disagreement concerning the most suitable English name. Sibley & Monroe (1990), Monroe & Sibley (1993), Clements (1991), Collar *et al.* (1994) and BirdLife International (2008) all use Orange-breasted Bushshrike. However, another widespread species *Chlorophoneus*

*sulfureopectus* is also known as Orange-breasted Bushshrike or Sulphur-breasted Bushshrike. To prevent confusion we prefer the unambiguous name Braun's Bushshrike, as employed by Fry & Keith (2000), Fry (2009) and Gill *et al.* (2009).

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- <sup>a</sup> A. P. Leventis Ornithological Research Institute, University of Jos, PO Box 13404, Jos, Plateau State, Nigeria. E-mail: michael@birdingafrica.com
- <sup>b</sup> DST / NRF Centre of Excellence at the Percy FitzPatrick Institute of African Ornithology, University of Cape Town, Rondebosch 7701, South Africa.
- <sup>c</sup> Flat 5, 63–67 St. George's Drive, London SW1V 4DD, UK.
- <sup>d</sup> Centro de Estudos e Investigação Científica UCAN, Rua Nossa Senhora da Muxima 29, CP 2064 Luanda, Angola.

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